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XLI.—*On the Minute Structure of the Recent* Heteropora neozelanica, *Busk, and on the Relations of the Genus* Heteropora *to* Monticulipora. By H. Alleyne Nicholson, M.D., D.Sc., F.R.S.E.

Part I.

The genus *Heteropora*, De Blainville *, has long been known to palæontologists as comprising a number of Jurassic, Cretaceous, and Tertiary fossils which have been generally, and are now universally, referred to the Polyzoa. Though the fossil species are abundant in certain deposits and are widely distributed, it is only quite lately that we have become acquainted with any recent forms of the genus. The first account of these was given by Mr. A. W. Waters (Journ. Roy. Micr. Soc. vol. ii. p. 390, pl. xv. 1879), who describes and figures a Japanese species under the name of *H. pelliculata*, sp. nov., and an Australian species under the name of *H. cervicornis*, d'Orb., sp. Very shortly after the publication of the paper just alluded to, Professor Busk described (from specimens which I had previously forwarded to him) another recent type of *Heteropora* from the seas round New Zealand, giving to it the name of *H. neozelanica* † (Journ. Linn. Soc. vol. xiv. p. 724, pl. xv. 1879). We have therefore now a

* Man. d'Act. p. 417 (1834).

† Mr. Waters informs me, in a letter, that, having examined specimens which I had sent him, he is of opinion that *H. neozelanica*, Busk, is identical with his *H. pelliculata*, the latter having the priority.

knowledge of the skeleton of excellently preserved recent and fossil species of *Heteropora*, though we are still unfortunately in total ignorance of the structure of the soft parts.

My own object in writing the present paper is quite a special one, and arises from the fact that the genus *Heteropora*, apart from its own intrinsic interest, has a peculiar importance in the eyes of palæontologists, owing to the well-recognized and remarkable external resemblance which it exhibits to the Palæozoic genus *Monticulipora*, d'Orb. So striking is this resemblance that very high authorities have employed it as one of their principal arguments for the removal of *Monticulipora* and its allies bodily to the Polyzoa, a transference which has been actually carried out in some works of great weight (as, for example, in Prof. Zittel's admirable 'Handbuch der Palæontologie," vol. ii. Lief. iv.). Not being myself, at present, prepared to acquiesce in the removal of *Monticulipora* to the Polyzoa, and being in possession of sufficient specimens of the recent *Heteropora neozelanica*, Busk, I determined to investigate for myself how far the resemblance between the two genera might extend as regards the details of their *internal structure*. With this view I prepared a series of thin sections of *H. neozelanica*, and have carefully studied these and compared them with precisely corresponding sections of various species of *Monticulipora*. In the present paper, then, I propose to give an account of the minute structure of the above-mentioned species of *Heteropora* and of two different types of *Monticulipora* (selected for different reasons), comparing these with one another, with the view of ascertaining how far they may agree with, or differ from, one another in fundamental characters. Before proceeding to this, however, it may be advisable to make a few very brief and general remarks on the genus *Heteropora*, and also to give a short account of the external characters of *H. neozelanica*, Busk.

The genus *Heteropora* is thus defined by Prof. Busk in his classical 'Monograph on the Fossil Polyzoa of the Crag' (1859) :—

"Polyzoarium erect, cylindrical, undivided, or branched ; surface even, furnished with openings of two kinds ; the larger representing the *orifices* of the cells, and the smaller the *ostioles* of the interstitial canals or tubes."

The essential character of the genus is thus the possession of a skeleton made up of *two* kinds of tubes, larger and smaller, the latter being the most numerous. The former have always been regarded as the proper *zoœcia* ; but the relations of the interstitial tubes or "*cancelli*" to the rest of the organism

have not been as yet satisfactorily established, though they have been usually regarded as serving in some way to place the cavities of the polypides in direct communication*. With regard to the internal structure of the genus, the existence of cross partitions or "tabulæ" in the tubes was long ago pointed out by Jules Haime, as regards his *H. conifera* and *H. pustulosa* (Mém. de la Soc. Géol. de France, vol. v. p. 208, 1854). Mr. Busk ('Crag Polyzoa,' p. 122) pointed out that the cancelli enter not at all or rarely into the central axis of the branches of the skeleton, this being made up of the thin-walled and polygonal proper zoœcia. The same observer also pointed out that the "ostioles," or apertures of the cancelli, are often "completely closed by a calcareous depressed lid, which in the majority of cases, however, is perforated in the middle;" and he expressed the belief that "the remains of these hymen-like lids," left behind at successive stages of growth, might probably account for the existence in the interstitial tubes of some species of "partial transverse, nearly equidistant septa," giving to the tubes in question a "peculiar moniliform aspect." Mr. Busk further indicated that in one species of the genus (viz. *H. clavata* of the Crag) "the interstitial orifices, or many of them, exhibit a stellate appearance, owing to the projection into their interior of numerous minute rays; affording thus another curious, false resemblance to a true coral." With this exception, nothing which could be compared with the "septa"† of the Cœlenterata has

* As the difference between the cancelli and the proper zoœcia is one of size and shape merely, and as both sets of tubes are precisely alike in their internal structure, it may be regarded as tolerably certain that the former were occupied by a set of zoöids essentially similar to those inhabiting the zoœcia, but modified or specialized in some way. On this view, the colony would be a truly dimorphic one. As for the perforated calcareous or chitinous opercula covering the mouths of the cancelli in parts of the skeleton (as described by Waters), we may suppose that these do not exist to begin with, but that they are developed in the last stages of the life of the zoöid, and that they are produced successively from below upwards as the area of active vitality is successively carried further from the fixed base of the organism (as we see to be the case in the coralla of various species of *Favosites*).

† Professor Busk, in his descriptions of the species of *Heteropora*, frequently employs the term "septa" to indicate the *transverse* plates which intersect the tubes of certain forms of the genus. Mr. Waters has followed Prof. Busk in this, or has sometimes employed the term "dissepiments" for the same structures. It need hardly be pointed out that these terms have such a totally different significance among the Cœlenterata, that their use in this connexion is undesirable, and is apt to lead to confusion. The term "*septa*," in fact, should be in all cases confined to the *radiating* and *vertical* elements of a calcareous skeleton; and the plates so named in *Heteropora* are the analogues of the "*tabulæ*" of the Cœlenterates.

hitherto (so far as I am aware) been noticed as occurring in *Heteropora*.

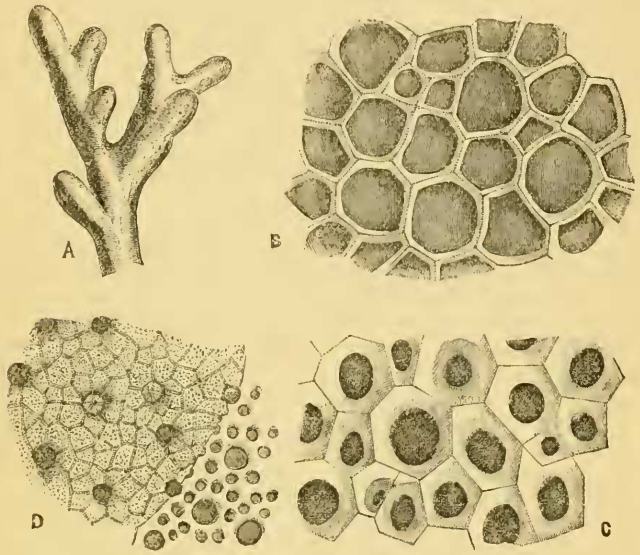
The above are the most important structural features which had been brought to light by the study of the fossil species of *Heteropora*; but our knowledge of the anatomy of the genus has been greatly extended by the investigation of recent species by Mr. Waters and Prof. Busk, as already referred to. The leading additional character which has been thus brought to light is that the walls of the zoœcia and cancelli (in the outer portion of their course) are perforated by numerous canals, which open into the cavities of the tubes by well-defined circular openings, thus placing contiguous tubes in direct communication.

Having now shortly passed in review some of the more important characters of *Heteropora*, so far as our present inquiry is concerned, I may next give a short account of the general features of *H. neozelanica*, Busk, before describing in greater detail its minute internal structure. The zoarium of this species (fig. 1, A) is "erect, composed of short divergent branches springing from a short thick stem, and soon dividing once or twice dichotomously, and terminating in blunt rounded extremities. The diameter of the primary branches is ·2 inch, and of the terminal ones about ·1 to ·15 inch. The surface presents orifices" (see fig. 1, B and C) "of two kinds, though scarcely distinguishable in size. The larger ones, in the older parts of growth, have a slightly raised peristome and are quite circular; the others (*cancelli*), disposed more or less regularly round these, generally to the number of seven or eight, are more or less angular, and the border of the opening is never raised" (Busk, *loc. cit.*).

Mr. Busk considers his *H. neozelanica* to be probably distinct from *H. pelliculata*, Waters, on the ground (1) of certain differences in the general form of the polyzoary, and (2) of the absence in the former of any external calcareous pellicle covering the surface, though there exists, in perfectly preserved parts of the specimen described, a thin chitinous covering closing the mouths of the tubes. Mr. Waters, as before remarked, is inclined to believe that the two forms are identical, in which case the name *H. neozelanica* will have to be abandoned. In fig. 1, B and C, I have figured the two states of the surface which my specimen of *H. neozelanica* exhibits, one of these being a reproduction of the excellent figure given by Prof. Busk (*loc. cit.*). I have also reproduced the figure given by Mr. Waters of the surface of *H. pelliculata*, as it shows characters which merit a moment's attention in this connexion. The left-hand portion, namely, of this

figure (fig. 1, D) shows the mouths of the interstitial tubes or cancelli, as well as some of those belonging to the proper zoœcia, to be closed by a thin calcareous pellicle, which is left after incineration, and which exhibits the peculiarity that it is perforated with numerous minute apertures opposite to the mouth of each of the interstitial tubes. The

Fig. 1.



A. A fragment of the polyzoary of *Heteropora neozelanica*, Busk, of the natural size (original). B. A portion of the surface of the same, apparently somewhat altered by maceration in sea-water, greatly magnified (original). C. A portion of the surface of the same (copied from Busk), apparently in a more nearly natural state, greatly magnified. Both B and C show the apertures of the zoœcia and cancelli. D. Portion of the surface of *H. pelliculata*, Waters (copied from Waters), enlarged 25 times, and showing the zoœcia and cancelli. In the upper part of the figure the cancelli (and the zoœcia partially) are closed by a calcareous pellicle, which is wanting on the right-hand side of the figure.

right-hand portion of the same figure shows the character of the surface, where the pellicle just alluded to has been removed. There can be no question that the existence of such a calcareous (or more usually chitinous) surface-pellicle, closing the cell-mouths, is a feature which speaks strongly for Polyzoan affinities ; but it should not be entirely lost sight of that very similar structures occur in certain extinct types

which would almost universally be referred to the corals, and which, at any rate, are very unlike the ordinary forms of Polyzoa. Thus it is well known that various species of *Favosites* (such as *F. Forbesi*, Ed. and H., var. *tuberosa*, Rominger, *F. turbinata*, Billings, and *F. clausa*, Rominger) are liable to have the mouths of the corallites closed by a calcareous pellicle, which may cover a large part of the surface of the colony.

It only remains to add, with regard to the general external characters of *H. neozelanica*, that the mouths of the tubes, even when fully exposed by maceration in sea-water (as in fig. 1, B), do not appear to show any signs of radiating spines ("septa"), though, as will be subsequently seen, such really exist in the interior of the cells. It may also be noted, as compared with any ordinary Monticuliporid, that though the skeleton is clearly dimorphic, in the sense that it is made up of two sets of tubes, the difference between the large tubes (zoœcia) and the small ones (cancelli) is small and sometimes hardly recognizable. The cancelli, in fact, are often nearly or quite as large as the proper zoœcia (see fig. 1, B and C); and the chief distinction between them rests upon the generally more clearly angular shape of the former, and upon their mouths not being at all raised above the general surface.

The minute Structure of the Skeleton of Heteropora neozelanica, *Busk.*

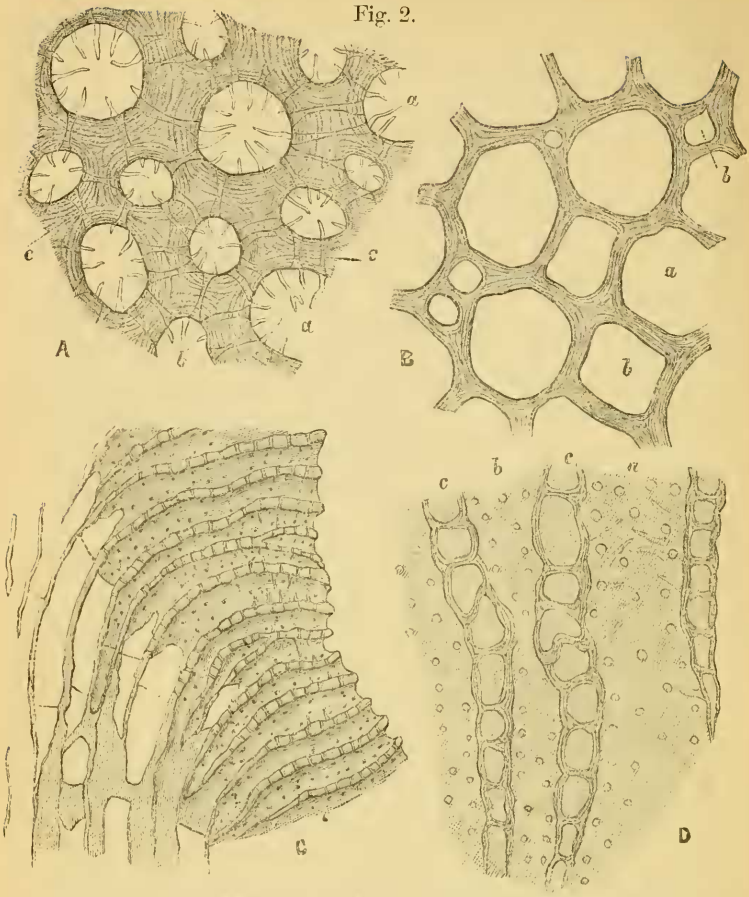
The skeleton of *H. neozelanica*, as of the species of *Heteropora* generally, is ramose or dendroid; and the branches resemble those of many similarly shaped corals in being composed of fasciculate tubes which are nearly vertical in the axis of the branch, but ultimately bend outwards to reach the surface. We can thus divide each branch into an *axial* and a *peripheral* or *cortical* portion; and not only do the tubes in these two portions of their course differ in *direction*, but they are markedly different (as we shall see) in their actual *structure*. That is to say, the structure of any particular tube is exceedingly different, according as we examine it in the axial or in the cortical part of its course. However, it is in the cortical portion of the skeleton alone, or almost alone, that the interstitial tubes are developed, the axis consisting wholly, or almost wholly, of the proper zoœcia. We cannot, therefore, arrive at a proper understanding of the true structure of *Heteropora* (or of any similarly constructed skeleton) without making *three* distinct sections, viz.:—one parallel to the surface *and just below it*, which we may call *tangential*, and which is the most important of all, as giving us the cross

section of the tubes in their final and most fully developed condition; secondly, one at right angles to the branch (a *transverse* section); and, thirdly, a *longitudinal* section, dividing the branch vertically through its median plane. The following are the principal points brought to light by an examination of these three sets of sections in *H. neozelanica*:—

(a) *Tangential sections.*—As just remarked, there are no sections which yield more interesting and valuable results than those which intersect the skeleton tangentially, just below the surface upon which the tubes open. When we examine such a section (fig. 2, A) we observe that it is generally quite possible to distinguish the proper zoœcia from the interstitial tubes by their size, but that these two sets of tubes are in no way distinguished from one another in point of structure, while their dimensions are often very nearly the same. The tubes are all rounded; and their walls are very thick, and are composed of delicate calcareous laminæ arranged concentrically around the cavity, and not showing any line of demarcation between each other. In this respect the walls have the structure of such species of *Monticulipora* as *M. ramosa*, *M. Jamesi*, &c., and differ altogether from such other species as *M. pulchella*. The most remarkable feature, however, in the structure of the wall consists in the presence of numerous canaliculi, which pass transversely across the thickened wall (fig. 2, A) and open at both ends by wide funnel-shaped apertures into the cavities of the tubes. In this way the zoœcia and interstitial tubes are placed in direct and free communication with one another throughout the entire colony. Sections of this nature also prove with absolute certainty that these canaliculi are strictly confined to the *walls* of the tubes—a point upon which, as will be seen, longitudinal sections might leave us in some doubt.

Another very interesting and important point brought out by tangential sections is that both the zoœcia and cancelli are provided in this part of their course with numerous delicate radiating spines, which spring from the wall (fig. 2, A) and are directed inwards for a longer or shorter distance, usually falling short of the centre. I am not aware that the presence of these radiating spinules has hitherto been recognized as occurring in the recent *Heteroporæ*, or in the extinct forms, except in *H. clavata*, Goldf. (according to Busk), and then only at the mouths of the interstitial tubes. In *H. neozelanica* they are very slender and delicate, and often break up in thin sections, so that they may appear to be wanting in a greater or less number of the tubes; but I have never failed to recognize their existence in some part or another of tangential

Fig. 2.



Thin sections of *Heteropora neozelanica*, Busk (recent). A. Part of a *tangential* section taken just below the actual surface, enlarged fifty times. The zoœcia are cut across in their outer thickened portion; and the canaliculi traversing their thick walls and communicating with the smaller interstitial tubes are well shown, as are the delicate radiating spines projecting into the cavities of both the sets of tubes. B. Part of a *transverse* section of a branch, showing the thin-walled angular condition of the zoœcia in the *axis* of the stems, the comparative paucity of interstitial tubes, and the total or almost total absence of connecting canaliculi in this region (enlarged 50 times). C. Part of the median *longitudinal* section of a branch (enlarged 18 times), showing principally the outer thickened portions of the zoœcia. The section shows distinct cross partitions (or "tabulæ") crossing the cavities of the tubes towards the deeper parts of the branch, as also the canaliculi crossing the walls, and the pores representing the openings of these on the backs of the tubes. D. Part of a transverse section in its outer portion, where the zoœcia are laid open *longitudinally* (enlarged 50 times). The section shows the peculiar structure of the thickened walls and the canaliculi crossing these. A few of the delicate radiating spines are also seen. *a a*, the proper zoœcia; *b b*, the interstitial tubes; *c c*, the walls, with the connecting canaliculi.

sections, and have no doubt that they are in this species really present throughout the whole of the peripheral part of the skeleton. Their special interest arises from their being in appearance precisely similar to the "septal spines" of so many species of *Favosites* (using the term "septal" in its proper signification).

(b) *Transverse sections.*—The appearances presented by transverse sections vary according to the part of the section which may be looked at. The central portion of such a section exhibits the tubes in the axial portion of the branch divided at right angles. In the circumference of the section, on the other hand, the tubes are divided more or less nearly longitudinally, owing to their curvature on nearing the surface, while this part also shows them in the thickened condition which they possess in the cortical portion of the branch. The appearances presented by the periphery of transverse sections are therefore the same as those shown in the corresponding region in *longitudinal* sections, and need not be considered till we come to speak of the latter. In the central region of a transverse section (fig. 2, B) we can study the condition of the tubes in the axis of the branches before they bend outwards to the surface; and we find that their structure is very different from that which they possess in the cortical region (as seen in tangential sections). Instead of being rounded and thick-walled, and provided with a largely developed canal-system, they are now thin-walled, and angular or polygonal in shape, and the canaliculi of the wall seem to have totally (or almost totally) disappeared. There is also an apparent total absence of the radiating spines which are developed in the cortical part of the tubes. Lastly, the tubes in this region appear to be almost entirely, or entirely, referable to the proper zoœcia, the interstitial tubes or cancelli existing only, or mainly, in the cortical region.

(c) *Longitudinal sections.*—These show precisely the same differences, as regards their central and peripheral portions, as have been already noted in transverse sections; but it is now necessary to briefly direct attention to both parts of the section (fig. 2, C and D). In the central portion of the section (supposing the slice to be taken in the median plane) the tubes are seen in the *axial* portion of their course, where they are nearly vertical, and where they exhibit the features which I have pointed out as characterizing them in the central region of transverse sections. That is to say, they are here provided with thin and delicate walls, in which the canal-system of the cortical region seems to be very slightly developed or wanting. The chief point to notice about the tubes

in this part of their course (and it is one that I have never failed to recognize) is that their cavities are here crossed by transverse calcareous plates or "tabulæ" (the "septa" of Prof. Busk and Mr. Waters), which, though few in number, are "complete" and in every way well developed* (fig. 2, C).

On the other hand, in the peripheral portion of their course (where the appearances are precisely the same as in the corresponding region of a transverse section) the tubes have very much thickened walls, and the walls are crossed at right angles by numerous canaliculi, which open at both ends into the cavities of the tubes by trumpet-shaped apertures. In all parts of the section, also, where the inner surfaces of the tubes are brought into view, these exhibit numerous rounded apertures or pores, which represent the mouths of the said canaliculi, and which have been well described and figured by Prof. Busk and Mr. Waters (*loc. cit.*). It is very difficult in the outer part of these longitudinal sections to distinguish between the proper zoœcia and the interstitial tubes or cancelli, their size being very much the same, and their internal structure being exactly alike; and this leads me to make a few remarks upon another point. When, namely, such a section as I now speak of is examined with the $\frac{1}{4}$-inch objective, it is seen that the wall separating contiguous tubes exhibits a central light space, limited on both sides by dark and definite boundaries, and crossed by the transverse canaliculi which have been already described (fig. 2, D). There is thus created an appearance of a central tube in the interior of the wall; or, rather, what I have here described as the *wall* might possibly be taken to be really *one of the smaller interstitial tubes divided longitudinally*. Apart, however, from the difficulty of conceiving how the canaliculi could be continued across and through the *cavity* of an interstitial tube, we have in tangential sections, as previously remarked, the conclusive proof that this is not the case, but that we really have to deal with the wall of the tubes. These sections, in fact

* Transverse partitions or "tabulæ" are well developed in various other Polyzoa (e. g. *Entalophora*, *Ceramopora*, and *Heterodictya*), but, of course, cannot be homologous with the "tabulæ" of the Cœlenterates. In a recent number of the 'Annals' (ser. 5, vol. vi. p. 244) Mr. Carter announces the discovery of transverse partitions or "tabulæ" in the well-known "stellate canals" of a *Stromatopora*, and adds that it is at once thus "proved that the *Stromatoporæ* could not have been sponges and that they were *Tabulate Corals*." This conclusion could only have been penned by Mr. Carter by inadvertence, since "tabulæ" occur not only in many corals, but also in various Hydroids, and, as just remarked, in several unquestionable Polyzoa, to which last group some good observers have referred the Stromatoporoids.

(fig. 2, A), prove, beyond a doubt, that the canaliculi are entirely confined to the *walls* separating contiguous tubes, whether these be the proper zoœcia or the cancelli.

So far as I have seen, no "tabulæ," or but an occasional one, seem to be developed in the outer thickened portion of the tubes; but it is often possible to recognize the delicate radiating spines or "septa," which are so well displayed in tangential sections. Lastly, owing to the unequal thickening of the walls of the tubes, it is not uncommon for the longitudinal section of their cavities to assume a beaded appearance, though this is not constant, and, when present, varies much in amount.

[To be continued.]

XLII.—*On* Stromatopora dartingtoniensis, *n. sp. with Tabulation in the Larger Branches of the Astrorhiza.* By H. J. Carter, F.R.S. &c.

[Plate XVIII.]

In 1878 I made the following statement, viz.:—"Thus in all essential points the structure of *Caunopora placenta* was the same as that of *Millepora alcicornis*," &c. ('Annals,' vol. ii. p. 313). I also stated that, in *Millepora alcicornis*, "the axial [structure], which in the transverse fracture only appears to be a cribriform surface, is now [in the opposite direction] found to be composed of longitudinal tubes in juxtaposition, more or less interrupted by tabulæ, and more or less pierced with holes by which they communicate with each other" *ibid.* p. 308). In 1879 I found that neither of these statements was tenable, but that the tubes of *Caunopora placenta* belonged to a separate organism, and that the "axial structure" was *Favosites Forbesii* (not *gothlandicus*, as first stated), over which the *Caunopora* had grown.

This year (1880) an article by Dr. F. Roemer has appeared in the 'Geological Magazine' for the month of August, in which the author states (p. 345) that "*Caunopora* of Phillips is not a good genus, but is founded on masses of *Stromatopora* which are perforated by vertical tubes not essentially belonging to *Stromatopora*," which tubes Dr. Roemer considers a form of *Aulopora repens*, having previously noticed what he published in 1844, viz. "that *Caunopora placenta* of Phillips was nothing else than *Stromatopora concentrica*" (p. 344); now, however, he adds, "My own observations confirm entirely the statement that the